

18. *Further Fossil Suidae from Hopefield*. By E. N. KEEN and R. SINGER, Anatomy Department, University of Cape Town.

(With Plates XXXIII-XXXV.)

INTRODUCTION

In a previous publication (Singer and Keen, 1955) the available suid material from the fossil site on the farm "Elandsfontein" was ascribed to a single new species *Meschoerus lategani*. Subsequently, on a number of field trips, one of us (R.S.) and a medical student, A. J. van Niekerk, recovered not only further specimens of the above genus, but also a fragment of a mandible containing deciduous third and fourth molars and a permanent unworn first molar (specimen S. 22) of this genus, as well as a second and third molar (probably upper) of a different genus, namely *Tapinochoerus*.

It is the purpose of this paper to describe the new material in the Anatomy Department:—

- A. The additional *Meschoerus* specimens so as to increase the range of variation in *Meschoerus lategani* and to evaluate the status of this species better, and to describe a specimen (S.28) of *Meschoerus paiceae*.
- B. The milk dentition in the fragment of mandible numbered S.22.
- C. The *Tapinochoerus* specimen (S.26) and to establish its specific rank.

DESCRIPTION AND DISCUSSION

A. Genus MESOCHOERUS Shaw and Cooke

DESCRIPTION

1. *Meschoerus lategani* Singer and Keen.

The general description of these four specimens (S.23, 24, 25, 27) is the same as in our previously published material (1955), and it is only necessary to note the specimens and their dimensions, and to outline any additional distinctive features.

Specimen S.23: A left upper third molar in which the posterior part of the talon consists of only one pillar behind the third lateral pair. This single pillar is vertically grooved as if in partial separation. The anterior median pillar and its outriders project beyond the root margin giving the tooth a pronounced rounded bulge anteriorly, well seen in side view (Pl. XXXIII A). On reviewing our specimens, this feature is seen in all the third molars particularly when in early wear. It is also observed in *Metridiochoerus* as well as in *Mesochoeus olduvaiensis* and *paiceae*, while in *Sus limnetes* from Omo (now classified as *Koiropotamus* = *Potamochoeus* by Hopwood and Hollyfield, 1954) the anterior median pillar and its outriders form a separate plate. In *Notochoerus* and *Phacochoerus* species the bulge is absent.

Specimen S.24: A left upper third molar in which the talon behind the third lateral pair consists of 5 small pillars. The buccal pillar of the second lateral pair also has an accessory nodule anterior to and confluent with it. Specimens S.23 and S.24 are in approximately the same stage of late wear, yet in S.23 the posterior pillars are fused into one massive posterior median pillar. This variation in number of pillars in the talon has already been commented on in our previous publication.

Specimen S.25: A right upper third molar whose front portion is missing as it is broken through the anterior pair of lateral pillars. The lingual surface of the 2nd and 3rd lateral pillars shows two deep vertical grooves, giving an exaggerated appearance not yet encountered in this species and suggestive of incomplete fusion of the cones which form the complex occlusal pattern of the teeth (Pl. XXXIII B). Viewed from the occlusal aspect the tooth presents an unusual concave curvature on the labial side of the posterior part of the tooth (Pl. XXXIII C) which is produced by a bulge at the crown-root junction of the 2nd lateral pillar. The roots are missing.

Specimen S.27: An almost complete right upper third molar. The anterior pair of roots are broken off, and a small piece of the central portion of the first lateral pillar on the lingual side is missing. The part of the talon behind the 3rd lateral pair in this massive tooth also consists of 5 pillars. The anterior median pillar and its outriders are so large as to almost form a separate plate, while the 2nd lateral pillar on the lingual side has an accessory cone in front of it (compare S.24) while the pillar on the buccal side has a small nodule projecting up in front of it at the cingulum. The buccal pillar of the 3rd lateral pair has 3 small accessory nodules on its outer side. The outer root of the 2nd pair of lateral pillars, though broken near its tip, is projecting back acutely to overlap and cover the plate-like roots of the 3rd pillar with which it is partially fused just below the crown-root junction (Pl. XXXIII D).

Specimen.	Maximum Length.	Maximum Breadth.	Occlusal Breadth.	Height of unworn pillars above root.
S.23	60.0	25.4	21.2	—
S.24	59.0	25.9	21.4	26.0 (posterior)
S.25	—	c.27	c.25	30.0 (posterior)
S.27	69.5	29.7	24.2	28.0 (posterior)
Range of previous specimens (7)	63-70	24-28	20-23	22-35

TABLE I: *Dimensions of the crowns of the upper third molars (mm.).*

The length of S.23 and S.24 might appear to exclude them from the range of variation revealed by the previous series. However, in the previously described series of lower third molars, of which 6 could be measured, the smallest was 67 mm. long, while the other 5 ranged from 73 to 77 mm. (mean 75 mm.), but there seemed to be no other reasons for excluding the short tooth from the series. In the same way, the shortness of S.23 and S. 24 will not exclude these two upper molars, identical in all other respects, from the species. The range of variation in length is now increased to 59-70 mm. Bearing in mind the following description of a different species of *Mesochœrus* from our site, and also that no upper teeth of *Mesochœrus paiceae* have previously been described for comparison, there is a possibility that the smaller upper teeth which we have included in our range for *Mesochœrus lategani* (e.g., S.24) may yet prove to be the uppers of *Mesochœrus paiceae*.

From table 1 it is also seen that S.25 and S. 27 are at the upper end of the range of variation for maximum breadth, and actually S.27 outstrips the other specimens and increases the upper end of the range to 29.7 mm.

2. *Mesochœrus paiceae* Broom.

Specimen S.28: A mandibular fragment containing a right third molar tooth in early wear. There are only 4 pairs of lateral pillars and these are more widely separated from each other than in *Mesochœrus lategani* specimens. The pillars taper to a pointed occlusal end, their bases being wide and partially fused at the cingulum. The 2nd lateral pillar on the labial side has an accessory cone anterior to it (Pl. XXXIII E). The anterior median pillar is pushed somewhat to the lingual side by a large outrider which is continuous with 6 low nodules fused together to form a plate anterior to the anterior median pillar.

Dimensions of S.28 (mm.):—

Maximum length	65.0
Maximum breadth	24.1
Occlusal breadth	17.7
Height of unworn 3rd pillar above root	31.5

The individual dimensions of this tooth fall within the previously reported range of *Mesochœrus lategani*, with the exception of the maximum length which is 2 mm. short of the lower end of the range. In itself this would have been of minor importance. However, there are only 4 pairs of well-separated lateral pillars, as compared with 5 pairs in *lategani*, and behind the fourth pair is a single undivided median pillar. In addition, despite its shortness, the breadth is at the upper limit of our previous range. Taking these 3 points into consideration, it cannot be distinguished from the 2 specimens (Broom's type and Shaw and Cooke's neotype) on which *Mesochœrus paiceae* is based.

DISCUSSION

Since our previous publication on the Hopefield Suidae, Hopwood and Hollyfield's monograph (1954) has been received. In this they classify *Mesochœrus* with *Hylochoerus*, hereby following Arambourg (1947), although the latter was not quite certain of this attribution. We have weighed up this opinion in the light of the reasons which led Shaw and Cooke (1941) to decide that their genus should be separated from *Hylochoerus*. Briefly, these were that the third molars were elongated and not so brachyodont as in *Hylochoerus*, and that the premolars were not reduced as in the modern animal. These points remain, in our opinion, ample justification for maintaining the genus *Mesochœrus* which now comprises three species, namely, *paiceae*, *olduvaiensis* and *lategani*. Leakey's *Mesochœrus heseloni* has been attributed by Arambourg (1947) to *Omochoerus*. However, Leakey (personal communication, 1955) still maintains that *Omochoerus* should be included under *Mesochœrus*. Consequently the position of *heseloni* is held in abeyance. On a phylogenetic sequence, *Mesochœrus* would seem a logical intermediate stage between *Hylochoerus* and *Metridiochoerus*. This problem may finally be resolved by further discoveries, particularly of tusks and other skeletal remains.

The specimen S.28, as described above, cannot be grouped with the previously described M. specimens of *Mesochœrus lategani*. Its dimensions and general appearance are such that it must be identified as *Mesochœrus paiceae*. In our previous series S.21 was included on the assumption that a 5th pair of lateral pillars was broken away posteriorly. Re-examination of this specimen, in the light of the fresh discovery, makes this seem less likely, and S.21 may represent a second example of a tooth which must be referred to the genotype *paiceae*.

B. MESOCHOERUS. Milk Dentition

Specimen S.22: A left mandibular fragment bearing an unworn M_1 , D_1 , and a root fragment of D_2 (Pl. XXXIV).

Dimensions of the fragment:—

Total length	77 mm.
Maximum breadth	24 mm.
Height of mandible at M_1	29 mm.

The *first molar* is unworn and is composed of 2 pairs of lateral pillars with a double median pillar between and separating them, small anterior outriders, and a large complex posterior median pillar. The posterior lobe of the tooth is broader than the anterior, and its 2 pillars are more separated from each other. The enamel is coarsely rugose and its irregularities form a pattern which is best seen on the labial side of the posterior lobe. The anterior and posterior lateral pillars fuse with each other about 4 mm. above the cingulum, and the posterior median pillar fuses with the posterior lateral pillar on both sides. The cingulum is only slightly developed. There are 4 roots which cannot be directly inspected as they are embedded in the mandible, but they were examined on a skiagram. The posterior roots are larger than the anterior.

Dimensions of M_1 (mm.):—

Maximum length	23
Maximum breadth (posteriorly)	13
Height of crown (anteriorly)	16
Height of crown (posteriorly)	15
Root length	c.15

Behind the tooth is a broad incomplete cavity which presumably contained the developing M_2 . The breadth of the mandible diminishes noticeably behind M_1 , and there are no signs of root canals from the cavity for M_2 .

The *last (fourth) deciduous molar* is a trilobed tooth with 3 roots on the labial side and 2 on the lingual side. It is in moderate wear. The 3 pairs of lateral pillars increase in size and decrease in wear from front to back. The 2nd lingual pillar is broken. The general appearance of the tooth is seen in Plate XXXIV. Examination of the fragment and of the skiagram reveals that the roots of this tooth straddle a cavity which one would have expected to contain the developing tooth germ of P_4 . This cavity communicates widely with the mandibular canal and it seems logical to assume escape of the tooth germ through this opening. A skiagram of the mandible of a modern domestic pig at about the same stage of development shows an unerupted tooth resting in a cavity at exactly the same position in relation to D_4 as in the fossil specimen.

Dimensions of D₄ (mm.):—

Maximum length	24
Maximum breadth at cingulum (posteriorly)	11
Maximum length of roots (from X-ray)	c.18

The *third deciduous molar* is only represented by a root fragment resting in one of the 2 alveolar root canals in front of D₄.

The bulk of the suid remains collected from Elandsfontein have proved to belong to the genus *Mesochoeerus*. The dimensions of M₁ of S.22 compare very favourably with those of the 2 worn M₁ teeth of *Mesochoeerus lategani* previously described, especially if the measurements are taken close to the cingulum. The unworn height of the crown (16 mm.) compares reasonably with the unworn height of M₃ (3rd pillar), which averaged 29 mm. in 4 specimens in which it could be accurately measured. The ratio of the unworn height of M₁/M₃ is thus 1:1.8. There seems good reason to conclude that this specimen is derived from a young *Mesochoeerus*.

C. Genus TAPINOCHOERUS van Hoepen and van Hoepen

Tapinochoerus meadowsi Broom

DESCRIPTION

Specimen S.26: A third and a second molar, found lying in apposition, were subsequently joined together with plaster-of-paris. The second molar is partially embedded in bone. The third molar resembles the tooth on which Broom (1928) originally based the species *Notochoerus meadowsi* (= *Tapinochoerus meadowsi*, Cooke, 1949). One of us (R.S.) examined specimens of *Tapinochoerus meadowsi* from the Transvaal Museum (S.K.? 387, S.K.? 388, B.F.1) now being studied by Dr. R. F. Ewer, Rhodes University, Grahamstown. The former two specimens are lower M₃ probably from the same jaw, and B.F.1 is a part of a skull, briefly described by Broom, 1948, containing unerupted M³ teeth and partially worn M² teeth. As a result of careful comparison, S.26 is considered to consist of left upper molars.

Left upper third molar: The general structure of the tooth is phacochoeroid consisting of two rows of lateral pillars separated by intermediate pillars. The anterior pair of lateral pillars is in full wear and constitutes the first lobe. The pair behind this is just coming into wear (Pl. XXXV). Posterior to this the unerupted portion of the tooth falls away sharply at an angle of about 45°. This part of the tooth consists of a large number of pillars (probably constituting 3 lobes) on each side with an intermediate pillar between

each pair. These lobes are less separated than the type specimen, but exhibit a similar appearance to S.K.? 387. The extreme posterior end of the tooth is broken off. The anterior lobe is broader than the second, and is rounded anteriorly in the occlusal view, with a slight constriction separating it from the 2nd lobe. The anterior extremity of the lobe consists of a number of circular and irregularly shaped nodules which cause an anterior bulging obvious in the lateral view (Pl. XXXV). The worn surface of the lateral pillars of this lobe are H-shaped with the inner pair of lobules equal in size and parallel to the outer pair. The bases of all the pillars are flattened from side to side, and are open; no roots are apparent. This is a typical phacochoeroid appearance. The cement covering the tooth is scanty.

Three third molar teeth from the Olduvai Gorge (Coryndon Museum, Old. B.K.II, Ex. 1953, nos. 109, 160, 448), studied by R. S., are almost identical in general appearance, with the posterior unworn part of the tooth falling away sharply at an angle of about 45° from the anterior plane of wear. The degree of separation of the pillars varies in the 3 specimens, being more marked in 109 and 448, but the same as S.26 in 160. However, in the latter the outer enamel is thicker and the tooth as a whole is broader.

Specimen.	Maximum Length.	Maximum Breadth.	Occlusal Breadth.	Height of worn anterior pillar.	Maximum Height.
S.26	c.74	21.5	19.2	63.8	70.0 (2nd lobe)
Type specimen	76	19	16	55	64
S.K.?387	—	19.1	15.7	53.1	68.3 (3rd lobe)
S.K.?388	—	19.1	15.9	53.0	c.67 (3rd lobe)
Old.B.K.II.109	—	19.5	16.8	—	—
Old.B.K.II.160	c.71	20.8	19.1	78.0	99.6 (3rd lobe)
Old.B.K.II.448	—	17.4	17.0	—	—

TABLE II: Dimensions of S.26 compared with those of other third molars (mm.). The height of 109 and 448 could not be determined precisely, but the maximum height was considerably in excess of 70 mm. The lengths of S.K.? 387 and 388 and Old. 109 were more than 65 mm. The Swartkrans specimens are not fully erupted; therefore less than full-grown length.

Left upper second molar: This closely resembles the M² of B.F.I which has not yet been described in detail (Broom, 1948). Our specimen is phacochoeroid in appearance and consists of 2 lobes which are less separated from each other than in B.F.I. Each lobe has a separate pair of roots. The anterior roots are smaller than the posterior ones, and the lingual pair smaller than the labial pair. There is a fairly well-marked cingulum anteriorly and the posterior aspect of the posterior lobe bulges back to meet the forward projection of the third molar. The bulge posteriorly of the heel is even more accentuated in B.F.I. The crown of the tooth is worn in the same plane as the anterior lobe of M² (Pl. XXXV).

The occlusal pattern of the anterior lobe appears to consist of 2 lateral pillars fused with an anterior median pillar, and the advanced stage of wear has left 3 enamel islands within an enamel outline forming two-thirds of a circle anteriorly and an irregular border posteriorly. The posterior lobe appears to consist of 2 lateral pillars which have fused in a most irregular manner with an anterior median, a middle and 2 posterior pillars (Pl. XXXV).

Specimen.	Maximum Length.	Maximum Breadth.	Occlusal Breadth.	Height above cingulum.
S.26	31.8	19.0	18.2	19.1 (anterior lobe) 22.3 (posterior lobe)
B.F.1	35.2	18.6	17.5	—

TABLE III: Dimensions of M² (mm.). In S.26 the maximum length is the same as the occlusal length. Height not measured in B.F.1 because junction between crown and root not clear.

There is no doubt that S.26 must be identified with the species originally named *Notochoerus meadowsi* by Broom (1928).

DISCUSSION

In efforts to reduce the number of genera of African fossil *Suidae*, Hopwood and Hollyfield (1945) and Arambourg (1947) found Broom's species difficult to place. Arambourg (1947) discussed the evolution of the phacochoeres in some detail and erected a phylogenetic series based on increasing height of the teeth, increasing length of the third molars, and decreasing separation of the constituent columns of the third molars. Assuming an origin in some ancestor resembling *Sus* or *Potamochoerus*, his series runs through *Hylochoerus* to *Metridiochoerus* Hopwood, and then *Notochoerus* Broom as a logical step to *Phacochoerus*. Without discussing the height or the poor separation of the columns of the tooth on which it was based, Arambourg agreed with Broom's original attribution of the species to *Notochoerus*. Hopwood and Hollyfield (1954), evidently unhappy with this opinion, included the species in *Metridiochoerus* Hopwood 1926. The height and length of the specimen, compared with those of the genotype *Metridiochoerus andrewsi*, make them uneasy companions.

A similar difference of opinion, in the opposite direction, shows that these authorities are not wholly in agreement over the definition of the two genera. Arambourg (1947) considered that *Notochoerus dietrichi* Hopwood 1934 should be included in *Metridiochoerus*; Hopwood and Hollyfield persist in the opinion that this is a *Notochoerus*.

The mean dimensions and characters of the upper and lower third molars in previously described *Metridiochoerus andrewsi* specimens may be summarised as follows: maximum length c.60 mm., length of talon (i.e. portion

behind the first 2 lobes) *c* 25 mm., maximum breadth 20-28 mm., unworn height of crown 50 mm. or less; roots fairly well developed. *Notochoerus capensis* third molars have the following characteristics: the tooth is greatly elongated (max. length 80-100 mm.) by development of the talon (length 50-70 mm.), maximum breadth is 22-30 mm., and unworn height is *c* 50-60 mm.; roots are well developed and lateral columns are fairly well separated from each other. The original *Notochoerus meadowsi* and those third molars which have been classified with it under the generic name *Tapinochoerus* may similarly be summarised: maximum length 70-75 mm., length of talon 35-40 mm., maximum breadth 15-20 mm., unworn height of crown 65-80 mm. Here the columns are closely packed and there is very little root formation, the tooth as a whole having a marked phacochoeroid appearance. The dimensions of the specimens noted and described in this paper increase these ranges. The degree of separation of the columns (pillars) in these specimens varies, but none exhibit the fairly marked separation of *Notochoerus capensis*.

These measurements, together with the general appearance of the teeth in question, make it in our view unjustifiable to classify *meadowsi* specimens as either *Notochoerus* (after Arambourg, 1947) or as *Metridiochoerus* (after Hopwood and Hollyfield, 1954). In the phylogenetic sequence *Metridiochoerus-Notochoerus-Phacochoerus*, the *meadowsi* specimens form a natural link between *Notochoerus* and *Phacochoerus*. We therefore prefer to retain the genus *Tapinochoerus* with two species, *meadowsi* Broom 1928 and *modestus* van Hoepen and van Hoepen, 1932. The latter, which is the genotype, is based on a considerably smaller third molar recovered from Cornelia, Orange Free State.

It might be argued that *Tapinochoerus* in this sense does not deserve separation from *Phacochoerus*. Cooke (1949) wrote: "Very possibly this may be regarded as only a sub-genus of *Phacochoerus*." Arambourg (1947) stressed the existence in early Quarternary times of a primitive form of *Phacochoerus africanus*, larger than the modern types and showing slightly greater complexity of enamel pattern. To this he gave the subspecific name, first used by van Hoepen and van Hoepen (1932), of *Phacochoerus africanus fossilis*. Whether this concept should be broadened to include the teeth under discussion is, in our opinion, doubtful. We prefer to regard the differences between these teeth and *Phacochoerus* as of generic rank.

CONCLUSION

The presence of a second genus *Tapinochoerus*, which at Olduvai is found in Beds II and IV and at Olorgesailie in deposits contemporary with the upper part of Bed IV, as well as two *Mesochoerus* species, one of which is similar to *olduvaiensis* found in Beds II and IV, tends to refute the previous

hypothesis of the persistence of an isolated species at "Elandsfontein" (Singer and Keen, 1955). Because *Tapinochoerus* and *Mesochcerus* have been recovered from various parts of South Africa (Vaal River, Swartkrans, Cornelia) as well as from East and Central Africa, it would now appear unnecessary to postulate isolation and subsequent evolution of a new species in the Cape. "Elandsfontein" at Hopefield therefore reflects the widespread distribution of at least these two suid genera.

The large number of species and genera on record at present may indicate that if a sufficient number of specimens were recovered the true intraspecific and intrageneric ranges of variation would appear, and would allow considerable merging of the closely overlapping types, so diminishing the number of genera and species recognized. On the other hand, it may reflect rapid evolutionary development in several directions produced by habitat and other selective factors.

The discovery of *Tapinochoerus*, which at Olduvai is relatively archaic, and, in the Vaal River sites is found in the younger gravels, strengthens the conclusion previously suggested (Singer and Keen, 1955; Singer, 1955) that the Hopefield deposits should be assigned conservatively to the early Upper Pleistocene period, equivalent to the interpluvial between the Kanjeran pluvial and the first Gamblian pluvial of East African chronology, a period now recognized as being the final phase of the Kanjeran pluvial.

SUMMARY

1. Four additional upper third molars of *Mesochcerus lategani* are described, thus increasing the range of variation of the species and improving the previously described diagnostic characteristics. Another specimen, identical to *Mesochcerus paiceae*, is described, and, a specimen previously included with *Mesochcerus lategani* is now referred to *paiceae*. There is also a short discussion on maintaining the rank of *Mesochcerus*.

2. The fourth deciduous molar and a first molar in a young *Mesochcerus* mandible are described.

3. Fossil M^3 and M^2 are identified with the species originally described as *Notochoerus meadowsi* by Broom (1928). Reasons are given for disagreeing with opinion expressed that this species belongs to *Metridiochoerus* or *Notochoerus* and for maintaining the use of the name *Tapinochoerus* to indicate a genus intermediate between *Notochoerus* and *Phacochoerus*.

4. The presence of *Tapinochoerus meadowsi* and 2 species of *Mesochcerus*, considered in conjunction with the other extinct and extant forms found on the farm "Elandsfontein" at Hopefield, strengthens our view that the deposit may be referred conservatively to an early Upper Pleistocene period.

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